Drought legacy interacts with wildfire to alter soil microbial communities in a Mediterranean climate-type forest

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HIGHLIGHTS

- Hotter drought and wildfire alter soil microbial communities.
- Fungal and bacterial richness and diversity decrease with increasing disturbance.
- Fungal communities were more responsive than bacteria to the disturbances.
- Key functional groups, e.g. mycorrhizal fungi, decreased after drought + wildfire.

GRAPHICAL ABSTRACT
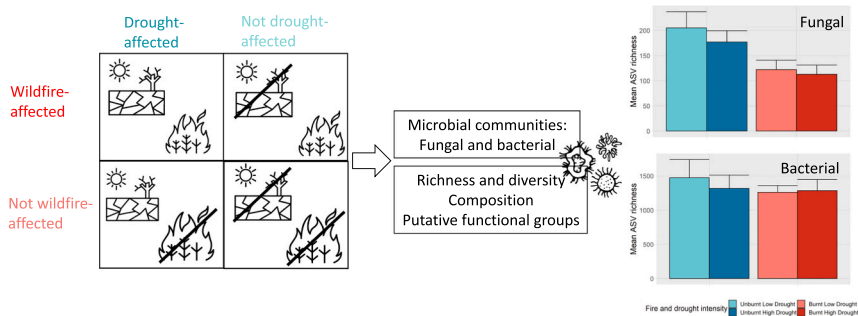
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ABSTRACT

Mediterranean forest ecosystems will be increasingly affected by hotter drought and more frequent and severe wildfire events in the future. However, little is known about the longer-term responses of these forests to multiple disturbances and the forests' capacity to maintain ecosystem function. This is particularly so for below-ground organisms, which have received less attention than those above-ground, despite their essential contributions to forest function. We investigated rhizosphere microbial communities in a resprouting *Eucalyptus marginata* forest, southwestern Australia, that had experienced a severe wildfire four years previously, and a hotter drought eight years previously. Our aim was to understand how microbial communities are affected over longer-term trajectories by hotter drought and wildfire, singularly, and in combination. Fungal and bacterial DNA was extracted from soil samples, amplified, and subjected to high throughput sequencing. Richness, diversity, composition, and putative functional groups were then examined. We found a monotonic decrease in fungal, but not bacterial, richness and diversity with increasing disturbance with the greatest changes resulting from the combination of drought and wildfire. Overall fungal and bacterial community composition reflected a stronger effect of fire than drought, but the combination of both produced the greatest number of indicator taxa for fungi, and a significant negative effect on the abundance of several fungal functional groups. Key mycorrhizal fungi, fungal saprotrophs and fungal pathogens were found at lower proportions in sites affected by drought plus

wildfire. Wildfire had a positive effect on bacterial hydrogen and bacterial nitrogen recyclers. Fungal community composition was positively correlated with live tree height. These results suggest that microbial communities, in particular key fungal functional groups, are highly responsive to wildfire following drought. Thus, a legacy of past climate conditions such as hotter drought can be important for mediating the responses of soil microbial communities to subsequent disturbance like wildfire.

1. Introduction

Chronic warming and drying and acute heatwave conditions associated with climate change have been associated with forest die-off events in many regions (Allen et al., 2010; Allen et al., 2015; Hartmann et al., 2018). These span all forested continents, and different climatic zones, species composition, and include tropical, temperate, Mediterranean, semi-arid and boreal ecosystems (Cobb et al., 2017). Global heating has also driven indirect impacts such as changing the fire season timing and length (Jolly et al., 2015) and increasing fire size and frequency in many regions (Brando et al., 2014; Hanes et al., 2019; Cattau et al., 2020). Recent catastrophic wildfires in Australia (Nolan et al., 2021), and elsewhere (2016 Canada, 2017 Chile, USA, and Portugal, 2018 Northern Europe, South Africa, and USA, 2019 Bolivia, 2020 USA) (Duane et al., 2021), as well as drought and heat induced-forest die-off events, underscore the need to understand how forest functioning will respond to the intersecting disturbances of drought and wildfire.

Research documenting disturbances (drought, wildfire, heatwaves, etc.) and their interactions is rapidly expanding, though, to date, the emphasis has disproportionately been vegetation and vertebrate fauna focussed, despite the widely recognised importance of belowground biota (e.g., Birnbaum et al., 2019). Microbial communities (such as fungi, bacteria, and archaea) are an integral part of forests and critical for ecosystem functioning and biogeochemical processes, including decomposition, nutrient cycling, carbon sequestration and storage (Hartnett and Wilson, 1999; Bardgett and Van Der Putten, 2014; Bass and del Campo, 2020; Lagueux et al., 2021). Fungi are essential decomposers because they convert recalcitrant organic matter into easier-to-digest forms that other organisms can use (Certini et al., 2021). Fungi also bind mineral particles together into more stable aggregates via long hyphae to enhance soil porosity and permeability (Rillig and Mummey, 2006; Certini et al., 2021). Root-associated mycorrhizal fungi form symbiotic relationships with >90 % of terrestrial plant species and improve plant uptake of water and nutrients (Sharma et al., 2013), assist with recruitment, increase plant biomass (Siefert et al., 2018; Lagueux et al., 2021) and protect host plants against drought (Augé, 2001; Akema and Futai, 2005), disease and stress (Newsham et al., 1995). Bacteria represent an important, though less explored, part of the microbial community in forest soils (Lladó et al., 2017). Bacteria contribute to a range of essential processes such as the decomposition of organic matter (Stursova et al., 2012), and N fixation (Reed et al., 2011). They also take part in decomposition of dead fungal mycelia and in rhizospheres of forest trees, and they interact with plant roots and mycorrhizal fungi as commensalists or mycorrhizal helpers (Lladó et al., 2017).

Soil microbial communities are highly responsive to drying and warming associated with climate change (De Vries et al., 2012; De Vries and Shade, 2013; Baldrian et al., 2023). Drought has been shown to impact activity and composition, likely due to high sensitivity to soil moisture changes, but microbial responses exhibit high levels of variation (Cregger et al., 2012; Bastida et al., 2017; Ochoa-Hueso et al., 2018). A large-scale precipitation manipulation experiment in semi-arid piñon-juniper woodland (*Pinus edulis- Juniperus monosperma*) in New Mexico, USA, showed that soil moisture was the main driver of the composition of soil microbial communities - fungal abundance in plots droughted for one year was 4.7 times greater upon wetting up (Cregger et al., 2012). In a global meta-analysis of the impacts of global change factors on soil microbial diversity and functionality, Zhou et al. (2020) found that reduced precipitation generally increased fungal richness but did not change bacterial richness. Fungi are thought to be more tolerant of water stress than bacteria due to their ability to accumulate osmo-regulatory solutes that do not impair metabolism, and their filamentous structure that facilitates substrate exploration (Brown, 1990; Manzoni et al., 2012). However, other studies have found the opposite pattern (e. g., Bastida et al., 2017). Exploring and understanding these varied responses of microbial communities to drought will improve our predictive capacity and management actions in the future (Birnbaum et al., 2019; Lagueux et al., 2021).

Wildfire can impact the survival and/or recolonisation of soil microbial communities in different ways; directly, via soil heating affecting the survival of mycelium and spores, and indirectly, by impacting the survival and growth of host plants, or by changing the physio-chemical properties of the soil such as pH, soil moisture and nutrient availability (Prendergast-Miller et al., 2017; Bowd et al., 2021). Bacteria generally resist direct fire effects better than fungi (Hart et al., 2005; Pressler et al., 2019) because although the immediate fire-induced changes in bacteria abundance and diversity often are substantial, recovery can be relatively fast due to rapid reproductive capacity (Certini et al., 2021). Fire effects on fungi are extremely variable, depending on their traits and tolerance, vegetation and soil type, and fire severity and frequency (McMullan-Fisher et al., 2011; Fox et al., 2022). The understanding of microbial communities, their associated functional processes, and fluxes in these in response to combinations of disturbances, such as drought and fire, is important for managing forests into the future, given that in some regions, these disturbances are predicted to increase in the future (IPCC, 2022). Advancing this understanding will depend on our ability to accurately characterize the plant-soil-microorganism relationship (Von Rein et al., 2016).

Mediterranean climate type ecosystems, given their climatic characteristics, may be vulnerable to projected changes in climate leading to increased aridity, such as higher drought, fire frequency and severe fire weather days (Batllori et al., 2013; Newbold et al., 2020; IPCC, 2022). Such multiple disturbances may have long-lasting impacts on ecosystem composition, structure, and function (Turner, 2010; Buma, 2015; Walden et al., 2023). Mediterranean southwestern Australia provides an important opportunity to study the impacts of chronic and acute droughts, heatwaves, and other disturbances, such as wildfire. The region has experienced chronic drying since the 1970s, an acute drought in 2010, followed by a series of heatwaves in early 2011 (Bates et al., 2008; Cai et al., 2011; Ruthrof et al., 2018). We took advantage of this regional event followed by a large wildfire in 2016 (the Waroona Bushfire – 69,000 ha) which burnt over impacted stands. This enabled us to sample wildfire and drought separately, and in combination alongside unimpacted controls (some areas had drought induced die-off and others did not; please see methods). Our overarching aim was to quantify the responses of soil fungal and bacterial communities to wildfire following a legacy of drought, in terms of species richness, diversity, composition, and functional types. We also examined community metrics of diversity and richness in relation to measured forest stand attributes to search for relationships between above and below ground dynamics. Our expectation was that wildfire following drought would significantly affect, and perhaps reduce, species richness, and abundance of important microbial functional types, particularly in the fungal community.

2. Materials and methods

2.1. Study site

The Northern Jarrah Forest (NJF) is in southwestern Australia and covers an area of 1,127,600 ha (Havel, 1975). The dominant canopy species are *Eucalyptus marginata* Sm. (1802), and to a lesser extent, *Corymbia calophylla* (Lindl.) K.D.Hill & L.A.S.Johnson (1995), with a midstorey dominated by *Allocasuarina fraseriana* (Miq.) L.A.S.Johnson (1982), *Banksia grandis* Willd. (1798), and *Persoonia longifolia* R.Br. (1810). The forest ranges from a tall, closed forest in the south, to an open dry sclerophyll forest in the northeast (Dell and Havel, 1989). The NJF occurs on laterite duricrust caprock overlying podzol clay profile with depths of ~30 m to >100 m, and a granite bedrock that occasionally forms outcrops (Churchward and Dimmock, 1989).

The climate is Mediterranean type, with cool, wet winters, and 80 % of rainfall occurring between April and October (Bates et al., 2008), and dry and hot summers, with drought periods lasting up to 4–7 months (Gentilli, 1989). A rainfall gradient exists across the region, ranging from >1100 mm yr-1 in the west, to ~700 mm yr-1 to the northeast (Gentilli, 1989). Over the last 50 years, the southwestern Australian region has experienced a chronic decrease in rainfall (reduction of 16 % in April–October rainfall since 1970, BOM/CSIRO, 2020), which is unique for the last 2000 years, with just two other earlier droughts of similar duration and intensity (Zheng et al., 2021) and with substantial variation in the past 700 years (O'Donnell et al., 2021). The region has also experienced a gradual increase in temperature (increase of 1.1 °C since 1910, DWER, 2021) and acute climatic events including droughts and heatwaves (Cai et al., 2011; Ruthrof et al., 2018). Recent work has shown that the number of days of >40 °C in the Capital, Perth, has doubled when comparing 1910–1939 and 1989–2018 (Breshears et al., 2021). Drought and heatwave events are predicted to increase in this region in the future (Hope et al., 2015; Andrys et al., 2017; Ukkola et al., 2020).

Acute drought and a series of heatwaves in 2010/2011 led to ~16,000 ha of the NJF experiencing varying levels of canopy die-off in early 2011 (Matusick et al., 2013). Sites severely affected were characterised by proximity to rock outcrops, high elevations, steep slopes, and lower water holding capacity soils, and were more clustered in xeric sites (Brouwers et al., 2013; Andrew et al., 2016). Additionally, drought-impacted sites examined using ERT (electrical resistivity tomography) were shown to have shallow bedrock and thinner soils (McGrath et al., 2023). In January 2016, part of the NJF experienced a lightning-ignited summer wildfire, the Waroona Fire (Ferguson, 2016; McCaw et al., 2016). The fire burnt 69,165 ha of native forest and farmland, destroying much of the town of Yarloop.

For this study, we chose 14 forest sites which are part of a broader network of research sites (Walden et al., 2023) (Fig. 1). Eight sites had experienced wildfire (four of which had experienced drought-induced forest die-off, and four which had not), and six sites were unburnt (three of which had experienced drought-induced forest die-off, and three which had not).

To determine the location of drought-induced die-off sites, several criteria were used. First, a model was developed by Brouwers et al. (2015) using data collected on the forest die-off event in the NJF in 2011 (Matusick et al., 2013). These data were used to create a map inferring drought and heat sensitivity to drought/heatwave events across the NJF, using elevation, distance to rocky outcrops, rainfall, temperature, and slope. The model was then used to delineate potential areas of pre-fire drought stress within the wildfire perimeter. The model was also used to choose sites that had a low probability of being impacted by drought. Second, sites were ground validated to ensure there were no signs of pre-wildfire drought stress, based on plant species association with drought: the midstorey tree, *Banksia grandis*, rarely occurs in drought/heatwave affected areas as they are more susceptible than other species to drought mortality (Matusick et al., 2013; Steel et al., 2019). Third, drought-affected sites were also characterised by structural evidence of the drought-induced canopy collapse reported by Matusick et al. (2013), with epicormic resprouts of a size that would have developed following this disturbance event (2011).

Based on measures of surface fuel consumption and remotely sensed fire severity, there was no evidence of difference in fire severity across
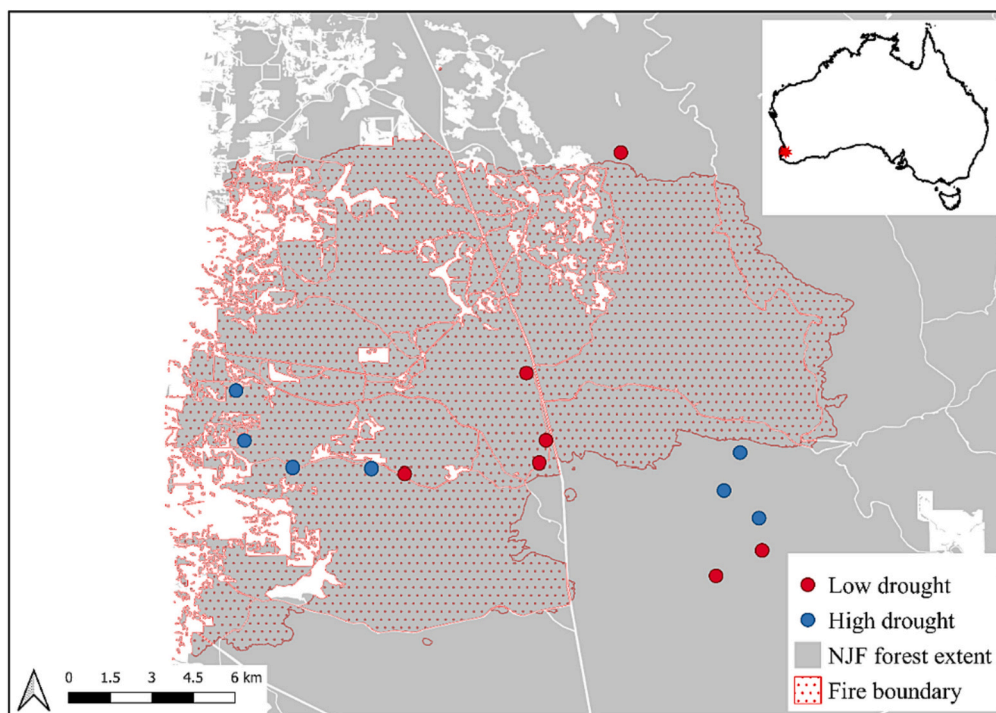

Fig. 1. Location of study sites located in the Northern Jarrah Forest (NJF forest extent, grey shaded area), southwestern Australia, including sites that were unburnt and burnt by wildfire, and affected by drought (low and high drought intensity). The stippled area indicates the Waroona Fire boundary.

pre-fire drought intensity conditions (see Walden et al., 2023 for details of image processing and generation of fire severity products). Therefore, there was no evidence of prior drought associated with systematic differences in fire severity enabling us to sample all conditions. Thus, the conditions presented a factorial design of drought and fire, and the two factors were largely independent from one other.

At each of the 14 sites, plots were established by Walden et al. (2023) following a modified Forest Inventory and Analysis assemblage (Bechtold and Scott, 2005). Each site contained four plots of variable radius, made up of a central plot with three plots orientated at 0°, 120°, and 240° from the central plot. The centre of each of these plots was at least 35 m from the middle of the centre plot. Plot configuration was altered only if the forest condition changed rapidly, or the subplot location fell on a track or road.

Above-ground forest stand variables were measured in 2016 as part of a larger study examining forest responses to drought and wildfire in this region (Walden et al., 2023) and were used to understand what may be influencing fungal and bacterial communities. In each plot, live canopy height (using a TruPulse 360 hypsometer, Laser Technology Inc., CO, USA) and diameter at breast height (DBH) were measured for each tree. Basal area (BA) was then calculated. In 2019, when soil samples were collected for this study (see below), canopy cover (using a spherical densiometer, after Lemmon, 1956) was measured at a subset of the plots, 1 m from the centre of each plot in each of the four cardinal directions, facing outwards.

2.2. Soil collection for microbial analysis

Soil was collected from beneath live, adult *E. marginata* trees in October 2019 (four years following the wildfire, and eight years following the drought induced forest die-off event). We purposely avoided the initial post-fire period to capture longer term trajectories. At four plots at each site, two *E. marginata* trees were chosen. Four soil samples, one from each cardinal direction, were collected from the rhizosphere (50 g each) from the top 5 cm of soil, 50–100 cm from the base of each tree. The four samples were bulked and placed into a labelled plastic bag. Soil samples were taken with a different sterilised plastic spoon for each tree. Samples were kept in an esky (cooler) with ice in the field before being transferred to a -20 °C freezer on the same day. Following storage, each bulked soil sample was homogenised and passed through a sterilised 2 mm sieve to remove leaves, pebbles, and fine debris in March 2021 prior to DNA extraction.

2.3. DNA extraction and sequencing

Soil samples from the two trees per plot were bulked to produce a total of $N = 56$ samples (16 for burnt + low drought, 16 for burnt + high drought, 12 for unburnt + low drought and 12 for unburnt + high drought). Total DNA was extracted from 0.25 g of the 56 soil samples using a PowerSoil DNA extraction kit (Qiagen) following the protocols specified by the manufacturer. Extraction controls (an extraction with no soil template added) and PCR negative controls (no sample added) were used to determine that there was no contamination during DNA extraction and amplification. Extracted DNA concentration was checked on a Nanodrop One spectrophotometer (ThermoFisher) for the threshold of a minimum of 5 ng•μL^{-1}, which was met in all instances except extraction controls, which had nil detectable DNA, prior to amplification.

All samples were sent to the Australian Genome Research Facility (AGRF) in Melbourne, Australia, for sequencing using Illumina MiSeq™. The ITS2 region was amplified from soil DNA using the primer fITS7 specific for higher fungi (Ihrmark et al., 2012) and the general primer ITS4 (White et al., 1990). To examine the bacteria present in the samples, the V3-V4 region of the 16S rRNA gene was sequenced using 341F and 805R primers (Herlemann et al., 2011; Wasimuddin et al., 2020).

2.4. Bioinformatics

Fungal ITS and bacterial 16S sequences were demultiplexed using the demultiplex function in the insect package (Wilkinson et al., 2018), and subsequent datasets were processed using the DADA2 bioinformatics pipeline in R 4.1.0 programming language (R Core Team, 2017) and RStudio v4.1.0 (Callahan et al., 2016; RStudio Team, 2021). ITS primers were removed from demultiplexed sequences using Cutadapt (Martin, 2011) due to variable sequence length of this region while 16S primers were removed within the DADA2 pipeline. All sequence reads were subjected to trimming, filtering, and quality control using the recommended settings where at the filter and trim step ITS merged pairs were dropped if below a minimum length of 50 basepairs while 16S sequences were kept for merged pairs between 280 and 275 basepairs. Retained sequences were clustered at the nucleotide level to amplicon sequence variants (ASVs). From these, bimeric, chimeric and singleton ASVs were removed using the nochim and de novo tools as indicated for DADA2.

ASVs were assigned putative taxonomy to the closest match (Callahan et al., 2017) from the custom curated and maintained reference databases (Unite 9.0 for fungal ITS (Abarenkov et al., 2023) and Greengenes v13.8 for bacterial 16S (Callahan, 2016)). All reads mapped to these reference databases were kept if identifiable to Kingdom, and those which were not identifiable at a Kingdom level or identified to the wrong Kingdom were considered unknown reads and were removed for downstream analyses.

Fungal ITS ASVs were designated into functional categories based on their putative life history following ecological guild assignment sensu FUNGuild (Nguyen et al., 2016). Only functional categories with probable confidence or higher were retained. Guilds used in this study included ectomycorrhiza (ECM), arbuscular mycorrhiza (AM), ericoid mycorrhiza (ericoid), saprotroph, endophyte, or pathogen. Where guild membership was complex (e.g. ECM and plant pathogen), ASVs were assigned membership in each relevant group. Bacterial 16S nutrient cycling functional groups were assigned using FAPROTAX (Louca et al., 2016a; Louca et al., 2016b) and the microeco package (Liu et al., 2021) to functions of ecological importance; carbon, nitrogen, sulphur, manganese, and hydrogen recyclers as well as cyanobacteria. Raw molecular data are stored at the Sequence Read Archive (SRA) curated by NCBI under the accession number PRJNA1014222.

The sequence table and taxonomic assignment generated in DADA2 were combined with a sample matrix using the package phyloseq (McMurdie and Holmes, 2013) for comparisons at the site and sample level. In phyloseq, negative control sequences were removed and using the prune_taxa tool. Only ASVs with >5 reads in 5 % of samples were retained for relative abundance statistical analysis. Read numbers were normalised to sample counts as a measure of relative abundance.

2.5. Statistical analysis

Our overarching aim was to quantify taxonomic and functional change in microbial communities in response to the hotter drought and wildfire and vegetation covariates. To achieve this, we present data and analyses at the community level and for functional groups within the microbial community with bacterial and fungal communities analysed separately. We undertook community analysis followed by regression of rarefied richness, diversity, and functional group relative abundance. We used indicator species analysis to identify ASVs associated with combinations of drought and fire. Finally, we conducted simple regression of forest stand metrics in relation to fungal and bacterial community indices (richness, diversity) to reveal above and below ground relationships.

All analyses were performed in the R 4.1.0 programming language (R Core Team, 2017) and RStudio v4.1.0 (RStudio Team, 2021) using phyloseq, glmmTMB (Brooks et al., 2017) and VEGAN (Dixon, 2003; Oksanen et al., 2017). Results were visually displayed using ggplot2

([Wickham, 2011](#)).

2.6. Community metrics and analysis

Shannon diversity and observed species richness of ASVs were calculated using the 'estimate_richness' function in phyloseq using all ASV counts. To assess compositional shifts in the microbial community in response to wildfire and hotter drought, non-metric dimensional scaling (NMDS) based on Bray–Curtis dissimilarity was carried out on relative abundance data generated from the ASV species matrix. To support the NMDS analysis and quantify differences in community composition among groups, we used permutational multivariate analysis of variance (PERMANOVA) using the 'adonis' function ([Anderson, 2001](#)) in VEGAN (999 permutations) to test for differences in community composition to wildfire and hotter drought and their interaction.

To test the effect of drought, fire, and their interaction, generalized linear mixed effect models were applied to community metrics (richness diversity) and relative abundance (overall and by functional group). The experimental unit was each plot, with a random effect of site (four plots per site) and fixed effects of drought, fire and their interaction using a Gaussian distribution (richness, diversity) or beta error distribution (relative abundance of functional groups). Data for arbuscular mycorrhizal fungi and sulphur recycling bacteria were too sparse for regression. We found no evidence of model violations after visually inspecting model residuals. We report effect estimate, standard error, t-value (richness, diversity), z-value (relative abundance) and p-value alongside means and 95 % confidence intervals.

To identify ASVs associated with each unique condition we used an indicator species analysis with function multipatt in R package indicspecies ([De Cáceres et al., 2010](#)). To supplement our understanding of

changes in relative abundance, we followed the approach of [Treseder et al. (2016)](#), calculating the change in frequency of occurrence for each functional group. We then calculated the percent change in occurrence with treatment. ASVs not occurring in either member of a pairwise contrast were excluded.

2.7. Above-ground vegetation and microbial relationships

To examine evidence for a relationship between microbial communities and above-ground vegetation, we conducted simple linear regression using microbial richness and diversity as response variables and forest stand metrics (live canopy cover, live canopy height, total basal area, live basal area, quadratic mean diameter) as reported in [Walden et al. (2023)](#). These simple linear correlations were calculated and are reported. Statistically significant correlations ($p < 0.05$) were taken as evidence of an association between above and belowground dynamics.

3. Results

3.1. Richness and Shannon diversity

Filtering resulted in 2,228,833 fungal sequences across 3821 ASVs in ITS and 3,520,253 bacterial sequences across 34,828 ASVs in 16S. Fungal phyla were Ascomycota (52.9 %), Basidiomycota (45.3 %), and Mucoromycota (1.6 %) with all other accepted phyla found in abundances of <1 % ([Fig. 2A](#)]. Most common genera included *Oidiodendron* (11 %), *Inocybe* (10 %), *Sebacina* (5 %), *Cortinarius* (5 %). Bacterial phyla were found in more diverse frequencies, consisting of Proteobacteria (31.4 %) and Actinobacteriota (29.8 %) followed by Acidobacteriota
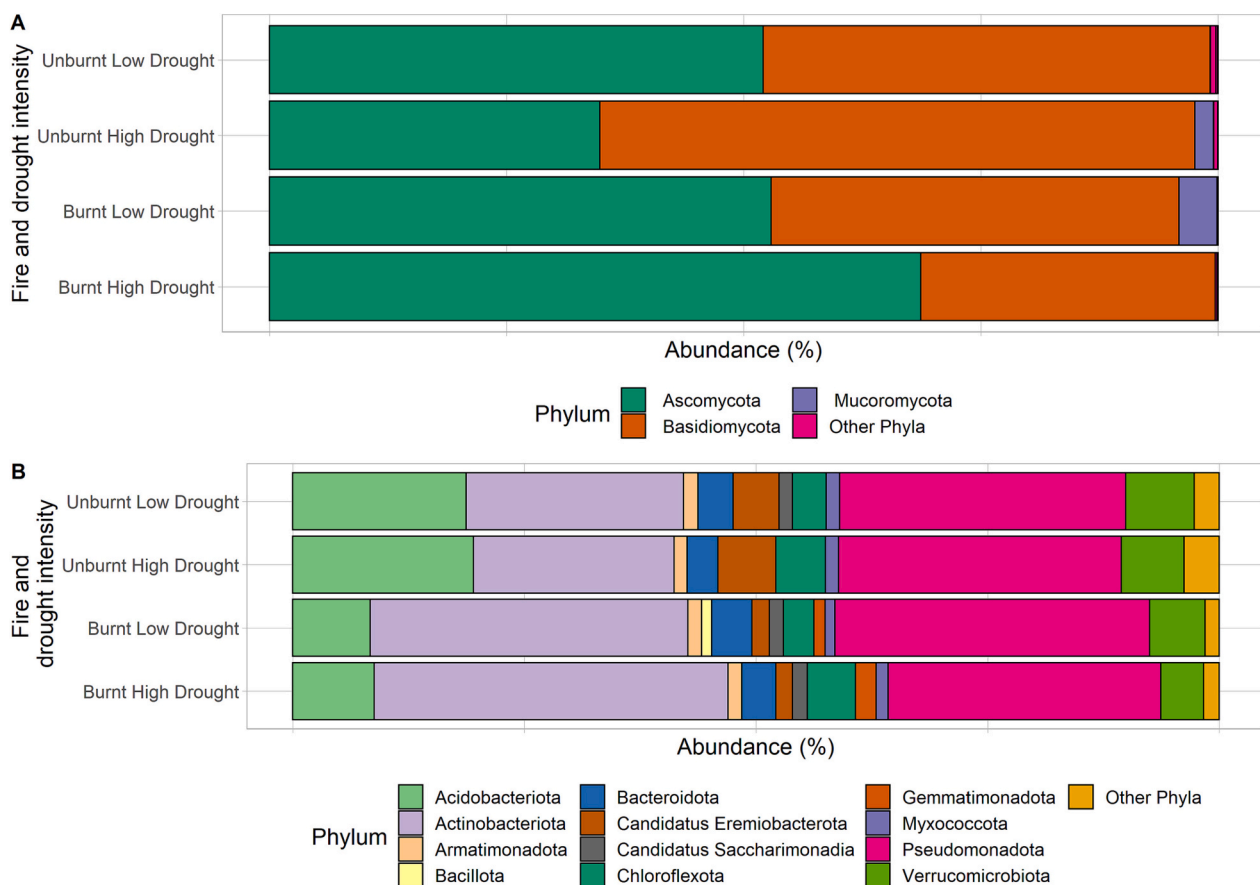

Fig. 2. Percentage average abundance of (A) fungal phyla, and (B) bacterial phyla, for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) in the Northern Jarrah Forest, southwestern Australia.

(13.4 %). All other phyla were found in abundances of below 4 % with 1 % unknown (Fig. 2B). Most common bacterial families included *Acetobacteraceae*, *Acidobacteriaceae*, and *Acidothermacaeae*.

The most common fungal phylum at burnt sites was Ascomycota while at unburnt sites it was Basidiomycota (Fig. 2A). Burnt sites contained higher abundance of the bacterial phyla Actinobacteriota, and unburnt sites had more Acidobacteriota (Fig. 2B).

Fungal richness and Shannon diversity decreased with increasing disturbance (Fig. 3A,B). Wildfire burnt sites had lower fungal species richness and diversity compared to unburnt sites (Fig. 3A; Table S1) (estimate = −82.9, SE = 19.5, t = −4.3, p = 0.002 and − 0.45 (0.22), t = −2.1, p = 0.04 respectively). Bacterial richness and Shannon diversity did not respond to drought or fire with no statistical evidence of differences among groups (Fig. 3C,D, Table S1).

3.2. Community composition

Disturbance type had a significant impact on fungal and bacterial community composition. The NMDS matrices of ASVs by sample unit had a two-dimensional solution with a stress of 0.214 and 0.143 respectively. Composition of the fungal community in the burnt sites was different from unburnt sites, and there was a difference between low drought and high drought (Fig. 4A) (ANOSIM, R = 0.534, p ≤0.001). Community composition of bacteria had a similar, but not as pronounced, pattern as the fungal community. Within both wildfire and unburnt sites low and high drought intensity sites had a significantly different bacterial community composition (ANOSIM, R = 0.624, p ≤0.001) (Fig. 4B).

3.3. Indicator species

We found significant indicators across fungi (51) and bacteria (745) for each combination of the treatments (Fig. 5). Similar patterns were evident across fungi and bacteria with the largest numbers of indicator "species" (ASVs) in the high drought category (when combining burnt and unburnt) with no indicators associated with unburnt, low drought plots. For fungi, burnt attracted 2.5× more indicators than unburnt but the pattern was more ~1:1 in bacteria (when comparing burnt vs unburnt). For bacteria, drought was far more important.

3.4. Functional groups

For fungi, the most consistent pattern was a negative wildfire and drought interaction effect (Fig. 6, Table S1). Overall abundance and ectomycorrhizal fungi, ericoid mycorrhiza, other saprotrophs, and other pathogens all possessed a negative drought and wildfire interaction (Fig. 6, Table S1). Overall abundance showed a marginally positive impact of wildfire while drought was associated with lower relative abundance of leaf saprotrophs and higher relative abundance of other saprotrophs. Most functional groups did not respond significantly (Fig. 6, Table S1).

In contrast to fungal functional groups, the interaction of drought and fire was not significant for overall abundance and only for one of the five analysed bacterial functions (positive effect with manganese recyclers; Fig. 7, Table S1). Overall relative abundance of bacteria was significantly higher in drought impacted plots (0.24, SE = 0.06, t = 3.9, p < 0.001; Table S1) and nitrogen and hydrogen recyclers also had
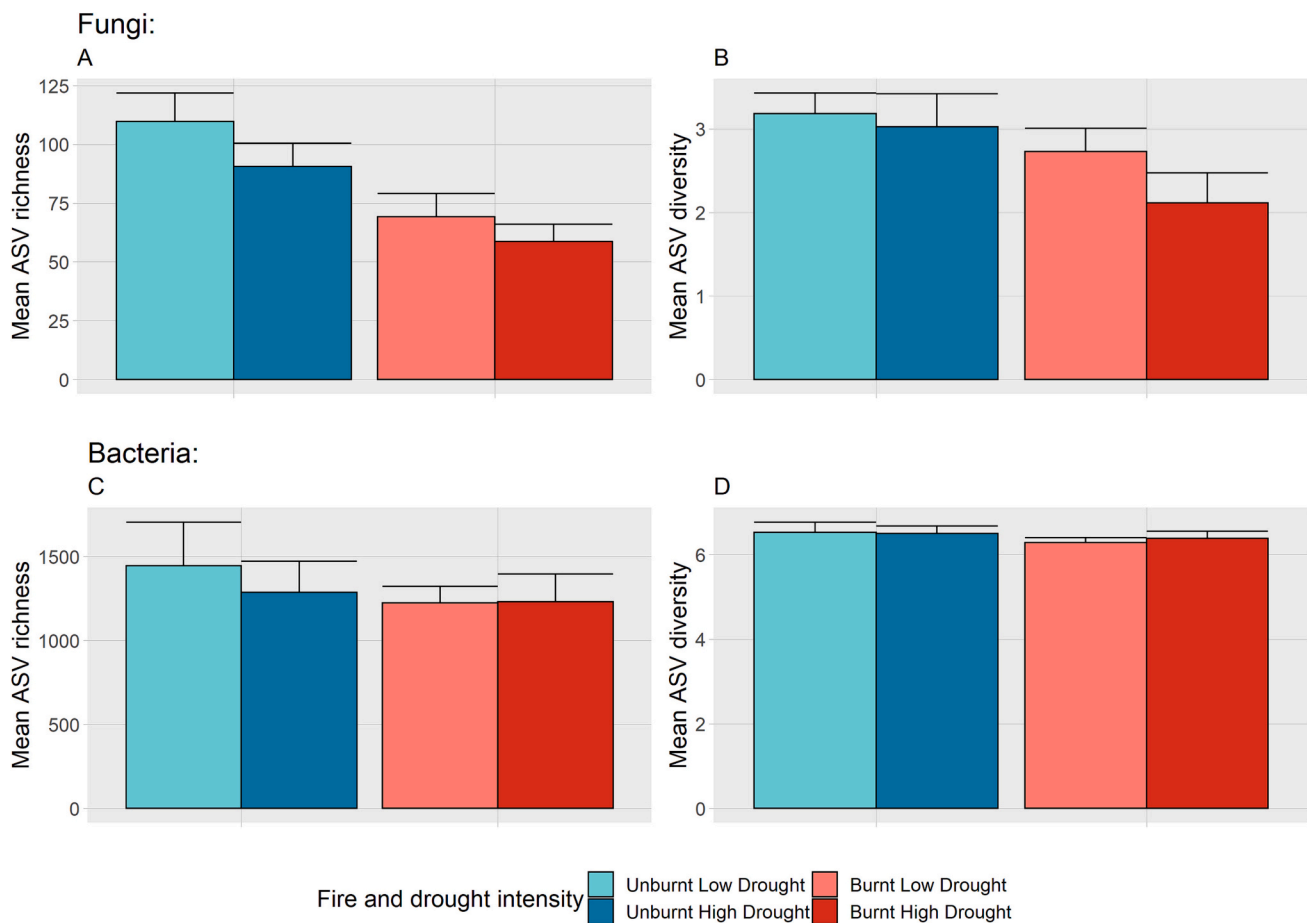

Fig. 3. Fungal species richness (A) and Shannon diversity (B), and bacterial species richness (C), and Shannon diversity (D) for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) in the Northern Jarrah Forest, southwestern Australia. Values are means and 95 % confidence intervals. Fungal richness and diversity declined with increasing disturbance while bacterial richness and diversity were stable.
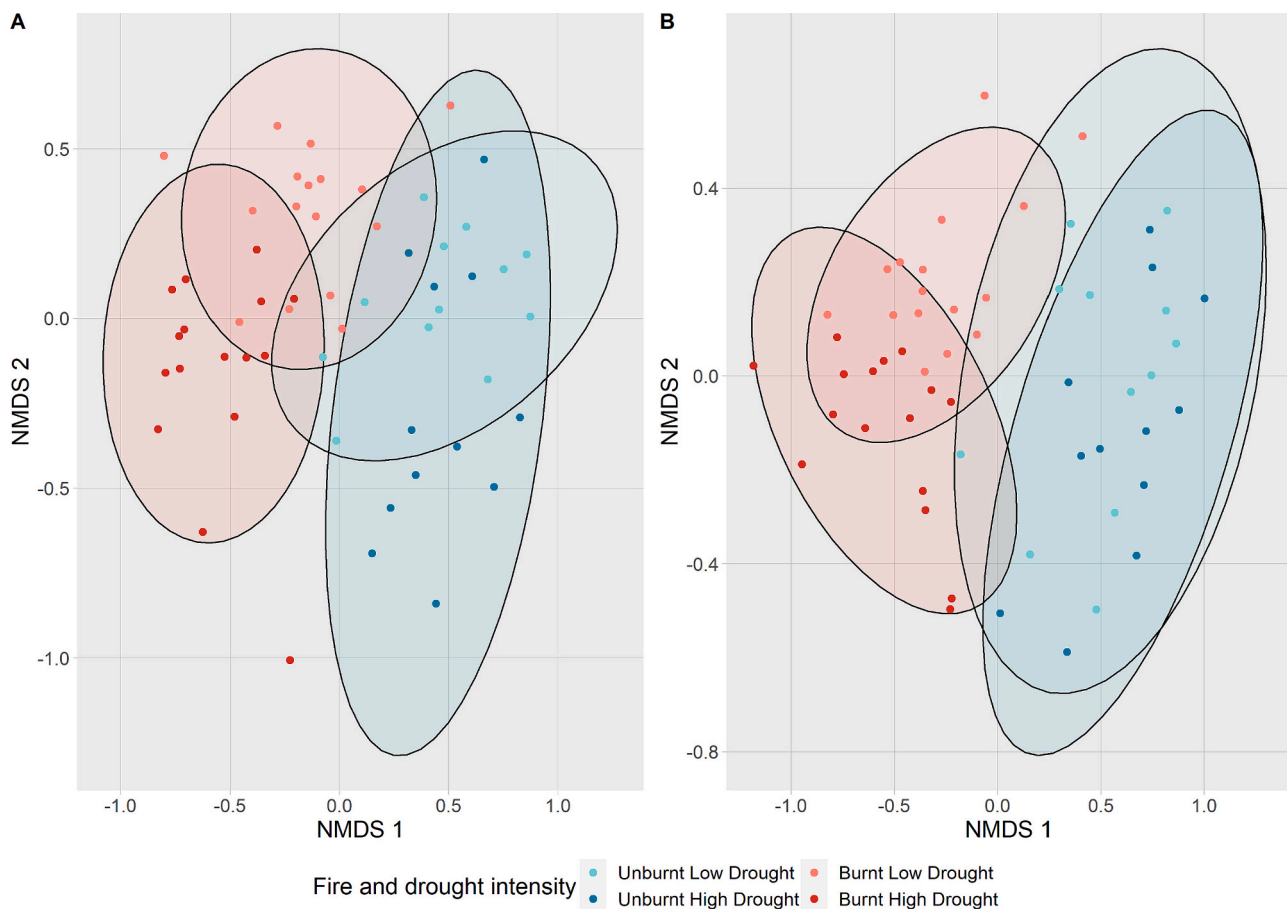
Fig. 4. Bray Curtis dissimilarity NMDS for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) for fungi (A) and bacteria (B) in the Northern Jarrah Forest, southwestern Australia. Ellipses indicate 95 % clustering. Both fungal and bacterial communities separated markedly with fire and occupied less graph space than drought alone.

Fig. 5. Indicator species for fungal and bacterial ASVs for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) in the Northern Jarrah Forest, southwestern Australia. For fungi, the combination of drought and wildfire produced the greatest number of indicator taxa, while for bacteria drought was more important.

higher relative abundance in drought impacted plots (Fig. 7, Table S1). No bacterial groups responded to fire alone (Fig. 7).

3.5. Above-ground vegetation and microbial relationships

Fire altered vegetation substantially more than drought (Fig. 8B, D,

F, H) with metrics differing between treatments based on lack of overlap of 95 % confidence intervals. Unburnt sites were characterised by higher live canopy height, live basal area, and canopy cover compared with burnt sites (Fig. 8A, C, E). Drought-affected sites that had been burnt had the lowest canopy cover of all treatments (Fig. 8C). Pearson correlation coefficients for bacterial richness and Shannon diversity relative to stand
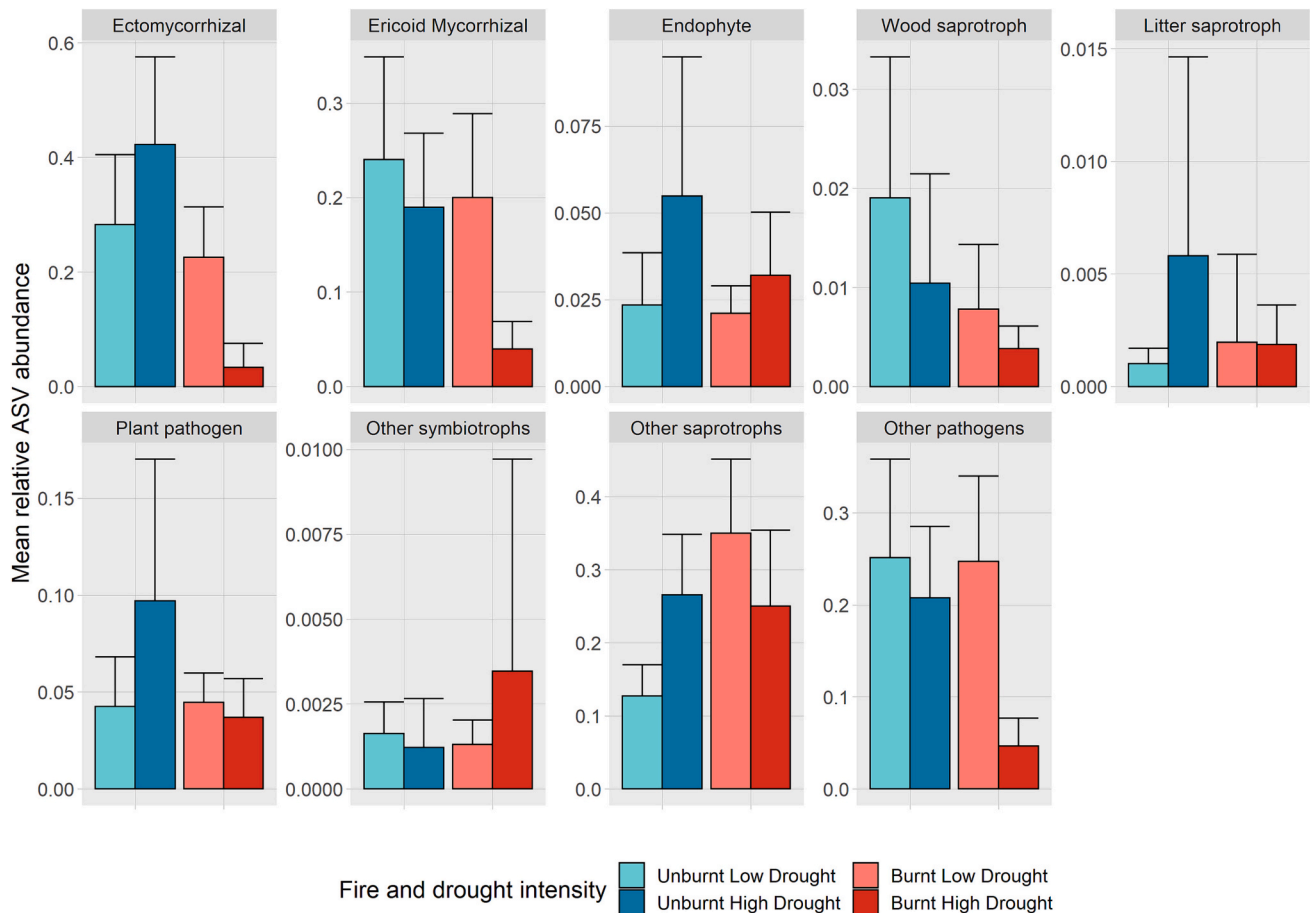
Fig. 6. Fungal functional groups for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) in the Northern Jarrah Forest, southwestern Australia. Values are means and 95 % confidence intervals. There was little evidence for an effect of drought alone, but the combination of drought and fire had a significant negative effect on abundance of four functional groups.

metrics (max height, live height, quadratic mean diameter live stems, canopy cover, live basal area, total basal area) were relatively small and ranged from 0.11 to 0.27 (*p* values >0.05; Table S2), except for quadratic mean diameter, all stems, which had a strong relationship with bacterial richness. For fungal richness and Shannon diversity, values ranged from 0.05 to 0.51 with strongest relationships between observed richness and live height (r = 0.51, p < 0.001; Fig. 8G). All correlation coefficients and their p-values are reported in Table S2.

4. Discussion

We have shown that microbial communities in a Mediterranean-type forest respond significantly to wildfire and drought, and particularly in combination. Specifically, fungal richness and Shannon diversity decreased with increasing disturbance, with wildfire having a significant impact. The fungal community was more affected by wildfire and drought than the bacterial community. We found distinct responses in community composition and functional groups, with a lower abundance of several key mycorrhizal fungal functional groups in drought plus wildfire-affected plots. There was a higher abundance of nitrogen and hydrogen bacterial recycler groups in drought-affected plots. Given that southwestern Australia is predicted to have an increased frequency and intensity of droughts and fire weather (Williams et al., 2009; Hope et al., 2015; BOM/CSIRO, 2020), our study provides important and timely insights into how microbial communities could respond to these disturbance events in this region.

4.1. Drought-affected sites

Drought alone did not significantly change the richness or Shannon diversity of microbial communities in our study. Consistent with our study, Zhou et al. (2020) found reduced precipitation does not significantly change bacterial richness. Other studies also show little change in bacterial richness in response to drought, suggesting that the bacterial community could be less sensitive to drought than fungi, which could be related to fungal communities' dependence on non-extreme moisture conditions (Hawkes et al., 2011; Bastida et al., 2017), though see Yuste et al. (2011) for fungi coping better with drought compared with bacteria. An alternative proposition, given our data were collected four years after fire and eight years after drought, is that bacterial communities respond and recover rapidly following moisture pulses compared with their slower growing fungal counterparts (Cregger et al., 2012).

Drought-affected sites, however, were associated with the largest numbers of indicator species (ASVs) for both fungi and bacteria. No indicator species were associated with unburnt, low drought sites. Fungal indicator species for drought only included *Talaromyces* taxa, which were also found in the drought treatment in a study of southwestern Australian Mediterranean-type shrubland (Birnbaum et al., 2019). *Talaromyces* spp. are known to be thermophilic and thermotolerant saprotrophs (Houbraken et al., 2012; Bowd et al., 2023). Drought also significantly increased the abundance of the functional group of other saprotrophs. In our previous study of drought-affected Northern Jarrah Forest sites, saprotrophs were also favoured under drought conditions, possibly due to dead roots in the soil associated with drought-affected trees (Hopkins et al., 2018). Saprotrophs are critical for
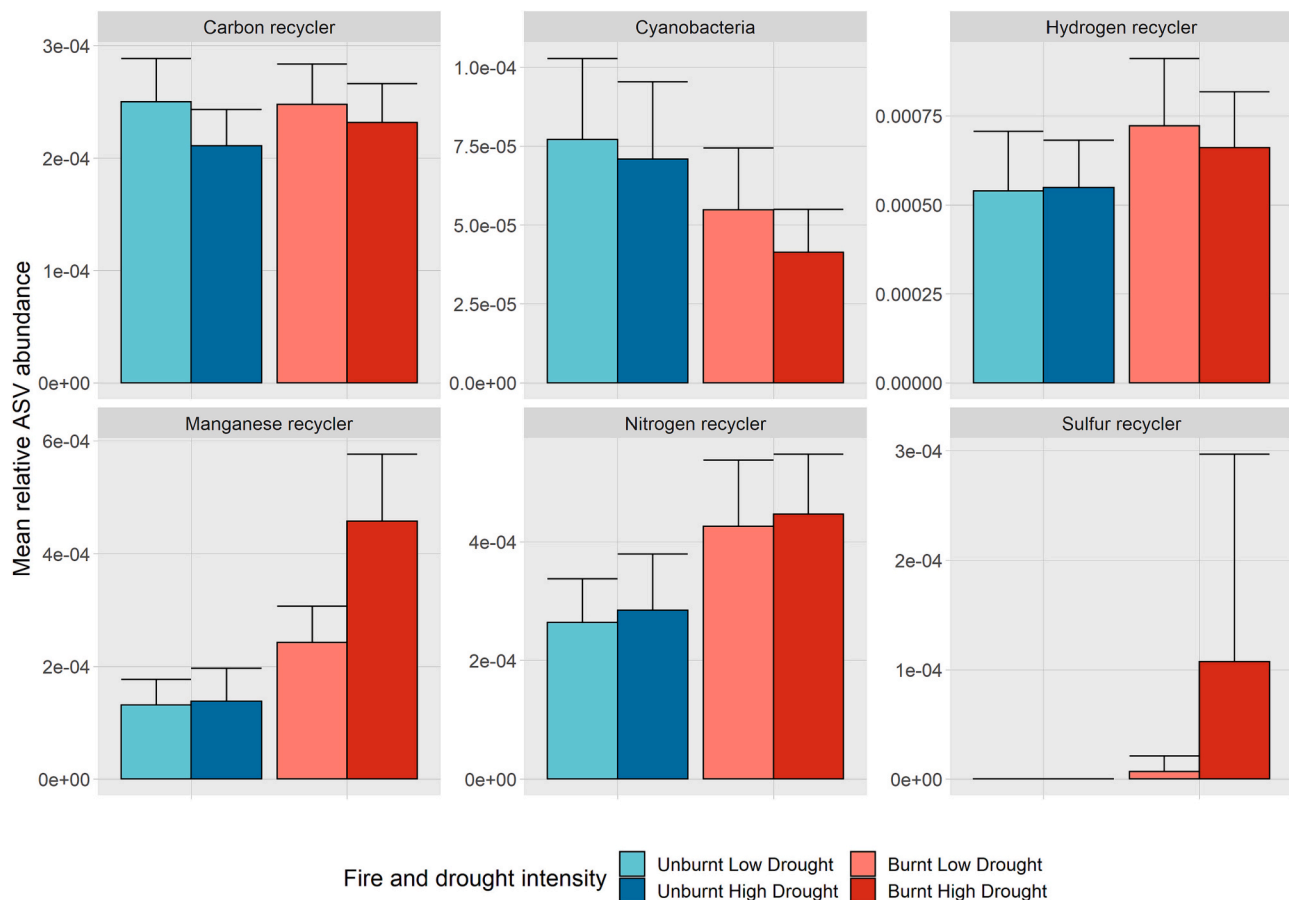
Fig. 7. Bacterial recycler groups for sites unburnt and burnt by wildfire (unburnt and burnt) and affected by drought intensity (low drought and high drought) in the Northern Jarrah Forest, southwestern Australia. Values are means and 95 % confidence intervals. Hydrogen and nitrogen recyclers responded positively to drought, and manganese recyclers to the interaction between drought and wildfire.

decomposition of litter and soil organic matter for nutrient redistribution (Baldrian et al., 2023) thus it is reasonable that their abundance would be higher in drought-affected plots.

Drought increased the abundance of bacterial recyclers, specifically, hydrogen and nitrogen recyclers. Hydrogen recyclers could be at higher abundance due to an increase in soil pH. In a global meta-analysis of peer-reviewed studies (2000–2019, 734 observations from 107 published studies) that examined the effects of drought on terrestrial productivity, drought stress increased the soil pH by 4.8 % (0.2 to 9.4 %; p = 0.04) (Wang et al., 2021). The same study indicated that soil nitrogen exhibited no significant responses to drought stress (p > 0.05). However, another meta-analysis on field studies that used rain-out shelters to reduce precipitation (37 studies), suggested that extractable NH_4+ increased by 25 % overall with precipitation reduction; and NH_4+ also increased significantly with increasing magnitude of precipitation reduction (Homyak et al., 2017). Clearly more work is needed to untangle the direct effects of drought, the implications for soil characteristics, and the indirect effects on bacterial communities.

4.2. Wildfire-affected sites

Wildfire alters the diversity and composition of microbial communities, directly, and indirectly, but how those changes are expressed are highly diverse and dependent on a range of factors including wildfire severity, ecosystem type, and disturbance history (Certini et al., 2021). In a review of multiple ecosystems, fire types and sampling methods, Dove and Hart (2017) showed that soil fungal communities (species richness and mycorrhizal colonisation) were adversely affected by fire. Sites in our study affected by wildfire four years previously, had lower

fungal richness and Shannon diversity compared with unburnt sites. A study from black spruce (*Picea mariana*) dominated boreal forest, northwest Canada, reported a similar pattern, where high fire severity caused a decline in richness and diversity of fungi one year after wildfire (Day et al., 2019). In a study of responses of fungal communities to fire in a dry sclerophyll eucalypt forest in south-eastern Australia, Bowd et al. (2023) also found that a short time (three years) since fire was associated with a decline in total fungal richness relative to a long time period (>26 years). We found burnt sites were dominated by Ascomycota and unburnt sites by Basidiomycota. This shift from the relative dominance of Ascomycota fungi in recently disturbed systems, to a gradual increasing abundance of Basidiomycota fungi over time post-fire disturbance has been noted in several studies (Sun et al., 2015; Ammitzboll et al., 2022) and may be related to Ascomycota possessing more genes associated with nutrition and carbohydrate metabolism than Basidiomycota, and hence giving them a higher stress-tolerance and competitive ability (Egidi et al., 2019). However, detailed and repeated microbial and floristic surveys are needed to investigate these patterns further.

Our study found a higher overall abundance of fungal functional types following wildfire, but no significant patterns in any individual functional type. The post-fire resumption of mycorrhiza from hyphal regrowth from root segments or viable propagules is often relatively fast, on the order of months (Alem et al., 2020), and mycorrhizal succession does occur over time (Treseder et al., 2004). In boreal forest in Alaska, for example, that burned 3, 15, 45, and 80 years earlier, dominant mycorrhizal groups shifted from AMF to ECM as succession progressed as fire did not noticeably reduce the abundance of AMF in contrast to ECM colonisation, which took 15 years to return to pre-fire levels
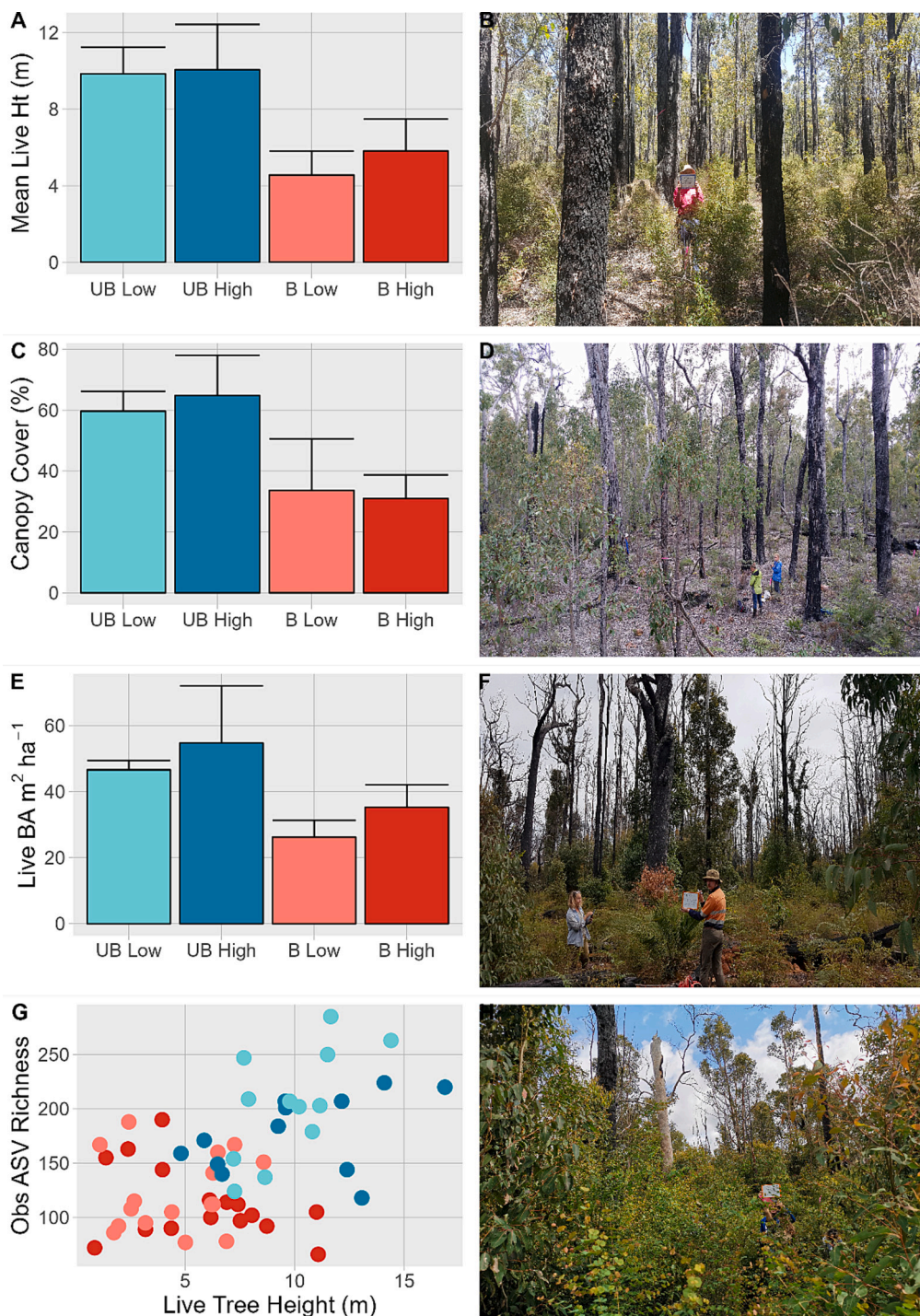
Fig. 8. Forest variables (A) mean live canopy height (m), (C) mean canopy cover (%), (E) mean live basal area (BA m^2ha^{-1}), (G) observed ASV fungal richness and live tree height (m), and photos showing examples from the study sites in the Northern Jarrah Forest, southwestern Australia, showing plots that were: (B) unburnt/ low drought intensity, (D) unburnt/ high drought intensity, (F) burnt by wildfire/low drought intensity, and (H) burnt by wildfire/high drought intensity. Values are means and 95 % confidence intervals.

(Certini et al., 2021).

Regarding bacteria, our burnt sites had a high abundance of Actinobacteriota (e.g., families: Mycobacteriaceae, Conexbacteraceae, Acidothermaceae, Pseudocardinaceae) and unburnt sites had more Acidobacteriota (e.g., Bryobacteraceae, Solibacteraceae). A lower acidobacteriota abundance in burnt areas is similar to published work from a range of forest ecosystem types. Bowd et al. (2022), found that recently burnt *E. pilularis* forest in southeastern Australia hosted lower abundances of Acidobacteria. A fire-induced decrease in Acidobacteria was

also recorded by Rodríguez et al. (2018) in Mediterranean forest ecosystems at 2–3 years post-burn. Adkins et al. (2020) assessed how three years after fire, Acidobacteria relative abundance was negatively related to burn severity in a Sierra Nevada (southwestern US) mixed conifer forest (unburnt sites 11.06 % vs burnt sites 9.22 %). Recovery post-fire has been recorded as strongest in phyla such as Actinobacteria, Proteobacteria and Firmicutes – a study three-months post-wildfire in a *E. melliodora/ E. albens* woodland in southeastern Australia showed that although fire has a significant effect on the bacterial community,

recovery was rapid and showed the microbial community was largely fire-tolerant (Prendergast-Miller et al., 2017). Actinobacteria has also shown strong post-fire recovery post-fire in chaparral in southern California, potentially favoured by an increase in soil pH, or increase in nitrogen and phosphorus availability (Pulido-Chavez et al., 2023).

4.3. Drought and wildfire-affected sites

Multiple disturbances, how disturbance regimes are changing, and the profound consequences of these for ecosystems is receiving increased interest (Turner, 2010; Buma, 2015; Agne et al., 2022; Davis et al., 2023). For example, how reduced rainfall due to climate change might affect the post-fire community is poorly understood in terms of the soil microbial community, which plays such an important role in the recovery of post-fire ecosystem functioning (Hinojosa et al., 2019). Rillig et al. (2019) reviewed over 1000 papers and examined the effects of an increasing number of global change factors (including temperature and water availability) on microbial communities, and found these factors caused increasing directional changes (e.g., a reduction in soil fungal ASV richness). In another study, it was shown that the combination of fire and drought disturbances can decrease soil total microbial biomass (Hinojosa et al., 2016). We found a monotonic decline in richness and Shannon diversity in the fungal community with increasing disturbance, while bacterial richness and diversity were relatively stable. The combination of drought and wildfire had a significant negative effect on the abundance of fungal functional types in general, and specifically, several main functional types. This pattern was particularly highlighted by a decrease in ECM and ericoid mycorrhizal fungi. Although not drought and fire per se, a study of drought and warming in the southwestern US using pinyon pine (*Pinus edulis*), found that the combined drought and warming treatment reduced the abundance and diversity of ECM more than either treatment alone (Gehring et al., 2020). A longer-term reduction in ECM has implications, especially for seedling recruitment, if multiple disturbances continue to occur in the future.

Other fungal saprotrophs and other fungal pathogens in our study were significantly reduced in abundance by the interaction of drought and wildfire. These types of saprotrophic fungi are important for the decomposition of dead organic matter, other fungi, dung or rotten wood on the forest floor, as well as some materials of animal origin (McMullan-Fisher et al., 2011). However, high severity fires can reduce the quantity of available substrates (Robinson et al., 2008). In our study, the combination of a drought-induced canopy die-off, eight years earlier, and the high severity wildfire could have reduced the available substrates that would normally be available to these types of saprotrophs. Reduced availability of substrates following wildfire leading to decreased abundance can also be applicable for pathogens, as seen in other studies, such as in Californian chaparral shrublands (Pulido-Chavez et al., 2023).

A significant response of fungal functional types to drought plus wildfire could also reflect underlying plot differences; similar drought-affected sites in the same forest as in this study are associated with shallow, rocky soils with lower water holding capacity, and located close to rock outcrops, at higher elevations, on steep slopes, and in xeric areas (Brouwers et al., 2013; Andrew et al., 2016; McGrath et al., 2023). Furthermore, drought-affected sites are characterised by the absence of a common drought-vulnerable midstorey species, *Banksia grandis*, and altered overstorey structure, including previous dieback (Matusick et al., 2013; Steel et al., 2019). These sites may thus have different microsite conditions, such as temperature (Dundas et al., 2021). In this context, it is of course, difficult to separate drought from other plot characteristics, and thus more controlled drought experiments are needed to investigate results seen here. More generally, understanding the effects of multiple disturbances such as drought plus wildfire remains an important challenge for microbial ecologists, and addressing it requires deconstructing compounded disturbances into their constituent drivers: nature,

intensity, frequency, and chronology (Philippot et al., 2021).

Our study also found a significant increase in the abundance of manganese bacterial recyclers with the interaction between drought and wildfire. This could be due to an increase in water-soluble manganese, which can increase after soil is heated to temperatures of 200 °C and above (Chambers and Attiwill, 1994). In that study, which examined post-fire conditions in *Eucalyptus regnans* forest, southeastern Australia, heating to only 100 °C caused no change in the concentration of manganese. In our study, the combination of drought site characteristics (e. g., shallow soils) may have made soil temperatures at these sites more extreme during wildfire, however, detailed studies will be needed to delve into this pattern further. In the Chambers and Attiwill (1994) study, the increase in manganese concentration was short-lived and decreased to control levels within two months; the authors postulated that this was possibly due to the rapid increase in the microbial population.

4.4. Future of forest functioning

Belowground microbial communities, such as mycorrhizal fungi, perform a wide range of critical ecosystem functions in forests (Van der Heijden et al., 2015). Disturbances such as drought and wildfire, and their interactions, can have multiple and complex implications for these ecosystem functions, including carbon cycling and storage and decomposition rates (Cregger et al., 2012; Bowd et al., 2022), as well as flow on effects on forest ecosystem resistance and resilience. Such implications are particularly concerning in regions such as southwestern Australia, which, under future climate scenarios, is predicted to experience further chronic changes in precipitation and temperature (Hope et al., 2015; BOM/CSIRO, 2020; DWER, 2021), extremes such as droughts (Hope et al., 2015) and heatwaves (DWER, 2021), and increased severity of fire weather and likelihood of increased frequency of wildfire (Williams et al., 2009). Given this broad and increasing range of potential disturbances on forest ecosystems, and their predicted increased frequency, the probability of multiple and interacting disturbances will also increase. In this study, we have shown a decrease in the abundance of mycorrhizal fungi with increasing disturbance. Whether this will lead to a decreased ability to support adult plants, as well as regeneration, is unknown. Only repeated monitoring of health and regeneration of these sites over longer time periods, across multiple and interacting disturbances, as well as investigations into the ability for these soils to directly support regeneration, may provide answers.

In conclusion, this study investigated the fungal and bacterial communities in a Mediterranean climate type, dry sclerophyll eucalypt forest that had experienced a hot drought eight years ago, and wildfire four years ago. We found a monotonic decline in richness and diversity in the fungal community with increasing disturbance, with the greatest changes resulting from the combination of drought and wildfire in two thirds of functional groups. There were distinct responses in community composition and putative functional groups to the disturbance types, with key mycorrhizal fungi (e.g., ECM, Ericoid), fungal saprotrophs, and fungal pathogens found in lower abundance at sites affected by the combination of drought and wildfire. Forest stand metrics (live tree height and canopy cover) were strongly correlated with fungal richness, suggesting above and below ground correspondence. Clearly microbial communities are affected by drought and wildfire in combination, which has implications for forest health, recruitment, and ecosystem function and forest persistence more generally.

CRediT authorship contribution statement

A.J.M. Hopkins: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing, Data curation, Visualization. **A.J. Brace:** Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing, Data curation, Validation,

Visualization. **J.L. Bruce:** Formal analysis, Investigation, Methodology, Writing – original draft. **J. Hyde:** Formal analysis, Investigation, Writing – original draft. **J.B. Fontaine:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **L. Walden:** Conceptualization, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **W. Veber:** Conceptualization, Investigation, Methodology, Writing – review & editing. **K.X. Ruthrof:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.170111.

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